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Downy Mildew of Spinach and Its Control

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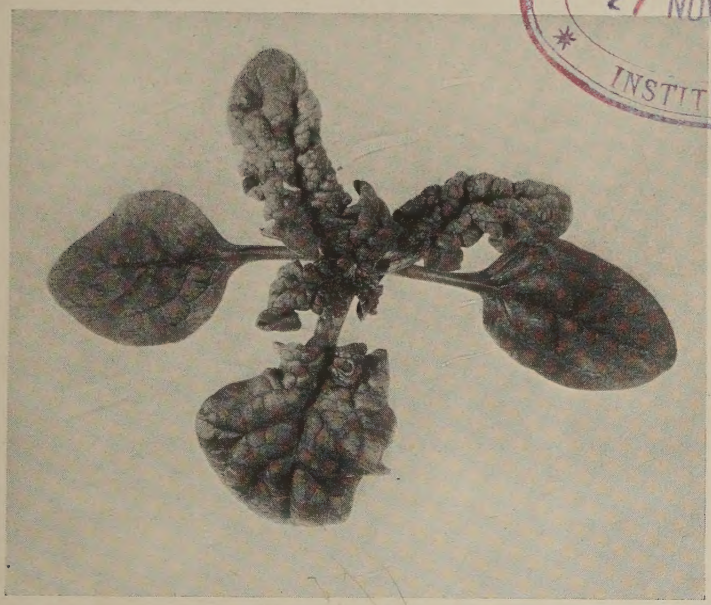

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CONTENTS

	PAGE
Suscepts	3
Plants affected	3
Varietal susceptibility	6
The disease	6
Names applied	6
History and range	6
Economic importance	7
Morphologic symptoms	9
Morphology of the pathogen	10
Etiology	13
Classification, name, and history of the pathogen	13
Pathogenicity	16
Life history	16
Sources of the primary inoculum	16
Sources of the inoculum for later cycles	18
Agents of inoculation	18
Factors which influence conidial germination	19
Ingress of the germ tube, and the infection courts	21
Period between inoculation and fruiting of the fungus	22
Epiphytotics of the disease	23
Control	24
Summary	25
References	26

DOWNY MILDEW OF SPINACH AND ITS CONTROL[1]

MATHIAS C. RICHARDS

Downy mildew of spinach, *Spinacia oleracea* L., caused by *Peronospora spinaciae* Laubert, was first described by R. K. Greville in England in 1824. Since then it has been found in nearly every country where spinach is grown. Frequently it causes severe losses to growers, but as yet no effective methods of control have been discovered, and relatively little is known regarding the life history of the pathogen or the conditions under which epiphytotics of the disease occur.

Because of the importance of spinach mildew in Nassau County, New York, studies on the disease and the causal organism were made during the years 1934 to 1938. The experimental work was done in the field in Nassau County and in the greenhouses and laboratories of the Department of Plant Pathology at Cornell University, Ithaca, New York.

SUSCEPTS

PLANTS AFFECTED

Spinach mildew was the first downy mildew to be described on any species of the Chenopodiaceae. Later as other plants in this family were found infected with downy mildew they were listed as suscepts of the spinach pathogen. Some workers went so far as to name plants not even closely related to spinach as suscepts. Plant species in the following families have been reported to be suscepts of the spinach fungus: Chenopodiaceae, Polygonaceae, Scrophulariaceae, Umbelliferae, and Violaceae. A list of the species named as suscepts is given in table 1.

Laubert (1906) made a careful study of the conidia and conidiophores of the pathogens found on spinach and on *Chenopodium album*. He concluded that the two fungi were distinct species. Gäumann (1919) agreed with Laubert and listed *Spinacia oleracea* and *S. inermis* as hosts for the spinach fungus. Both Laubert and Gäumann used morphologic differences of the fungi for determining species.

A few workers made careful cross-inoculation studies with the spinach fungus and with other Peronosporaceae found on species of the Chenopodiaceae. Schaffnit and Volk (1927) could not infect spinach with the pathogens taken from *Chenopodium album* and *Atriplex hortensis*. Hiura (1929) was unsuccessful in obtaining infection in cross-inoculation trials with the fungi from spinach and from *C. rubrum*. Leach (1931) could not obtain infection of swiss chard or of the following beet varieties: Detroit Dark Red, White Silver, and Giant Lucullus. He was unable also to infect

[1]Also presented to the Faculty of the Graduate School, Cornell University, June 1938, as a major thesis in partial fulfillment of the requirements for the degree of doctor of philosophy.

AUTHOR'S ACKNOWLEDGMENTS. The writer wishes to thank Dr. Charles Chupp for his helpful suggestions during the course of the investigations and Dr. H. M. Fitzpatrick for reading and criticising the section dealing with the nomenclature of the pathogen.

He is indebted to the Nassau County Farm Bureau Association for its support of the Fellowship which made these studies possible, and to the vegetable growers in Nassau County whose cooperation contributed much to the success of the work in the field.

two varieties of spinach, Prickly Winter and Long-standing Savoy with *P. Schachtii* Fuckel. Cook (1936) failed to obtain infection when he cross-inoculated with conidia from *C. album* and *Spinacia oleracea.* Halsted (1890) reported unsuccessful infection of violets with *P. effusa* (Grev.) Rabh.

TABLE 1. SUSCEPTS REPORTED FOR THE SPINACH MILDEW PATHOGEN

	Caspary (1855)*	de Bary (1863)	Fuckel (1868)*	Smith (1885)	Leunis-Frank (1886)*	Magnus (1887)	Saccardo (1888)	Schröter (1889)*	Halsted (1890)	McBride and Hitchcock (1890)	Williams (1891)	Fischer (1892)	Berlese (1903)	Laubert (1906)	Wilson (1908)	Clinton (1915)	Eriksson (1918)	Gäumann (1919)	Anonymous (1920)	Ferraris (1928)	Dana (1929)
Atriplex sp.:					×	×															
A. hastata							×	×				×	×		×						
A. hortensis																					
A. nitens							×	×				×									
A. patula	×	×	×				×	×				×	×				×				
A. roseum							×	×				×	×								
Beta vulgaris																			×		
Chenopodium sp.:				×	×	×									×						
C. album	×	×	×				×	×	×	×	×	×	×		×	×	×			×	
C. album-viridi																					
C. Bonus Henricus												×	×								
C. Capitatum			×																		
C. ficifolii																					
C. glaucum							×	×				×	×				×				
C. hybridium	×	×	×				×	×		×	×	×	×		×		×				
C. leptophyllum															×		×				
C. murale							×	×				×	×				×				
C. polyspermum	×						×	×				×	×				×				
C. rubrum													×		×						
Daucus carota									×												×
Persicaria sp.				×																	
Polygonum sp.:																					
P. convolvulus							×														
Spinacia oleracea:	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
S. inermis									×									×			
Viola sp.																					

*These data were taken from Laubert (1906); the original papers were not seen by the writer.
Synonyms: *Spinacia oleracea* (*S. spinosa*); *Chenopodium capitatum* (*Blitum capitatum*).

To determine the suscept range for *Peronospora spinaciae,* plants from several species and genera of the Chenopodiaceae were grown in the greenhouse at Ithaca and inoculated with viable conidia of the pathogen (table 2). The following method was used in making the tests: newly formed conidia were washed from infected spinach leaves with distilled water from an atomizer. The suspension of the conidia was then sprayed on both leaf surfaces of the test plants. The plants were inoculated in a chamber and left there, at greenhouse temperatures (65° to 75° F.) for forty-eight hours. They were then removed and placed on a bench in the greenhouse for ten days, after which they were again placed in the moist chamber. Infected spinach plants used as checks showed signs of the disease within twelve hours after they were replaced in the moist chamber. No signs or symptoms of mildew were found on the other plants. The inoculation studies

(table 2) indicate that for the plants tested only spinach and its horticultural varieties were susceptible to *Peronospora spinaciae.*

TABLE 2. SUSCEPT RANGE STUDIES MADE IN THE GREENHOUSE, 1937–38

Plants inoculated	Inoculated–*		Infected leaves*
	Plants	Leaves	
Allenrolfea occidentalis	30	300	..
Amaranthus sp. (fire):	40	210	..
A. Han Tsai	42	179	..
A. speciosus aureus	23	133	..
Atriplex hortensis atrosanguineus:	3	18	..
A. patula var. *hastata*	15	146	..
A. rosea	46	368	..
Beta vulgaris:			
Egyptian Flat	46	151	..
Early Wonder	12	68	..
Detroit Dark Red	32	112	..
Perfected Detroit	15	80	..
Mangel, Long Red	32	165	..
Swiss chard	25	116	..
Bassia hyssipafolia	31	598	..
Chenopodium album	13	110	..
C. Bonus Henricus	12	75	..
C. botrys	32	152	..
C. glaucum	23	114	..
C. hybridium	3	60	..
C. paganum	15	340	..
Kochia scoparia	3	350	..
Salsola pestifer	60	1200	..
Spinacia oleracea:			
Blight-resistant	18	78	72
Long-standing Bloomsdale	12	75	69

*Results from three trials.

In two tests the writer was unable to infect spinach plants when he inoculated them with conidia taken from *Chenopodium album* and *C. paganum.* This agrees with the findings of other investigators as reported on page 3.

Studies on infection were made in the field, and it was found that many chenopodiaceous weeds growing in or along spinach fields were severely infected while the neighboring spinach plants were not. In some spinach fields 95 per cent of the plants were infected with mildew; yet species of Chenopodium growing in these fields were free from mildew or only a few of the plants showed infection. Conidia and conidiophores taken from these weeds and observed under the microscope differed morphologically from those taken from spinach. When mildew was found on both spinach and chenopodiaceous weeds it was evident that two or more species of Peronospora were involved.

From the twenty species of plants inoculated with the conidia from *Peronospora spinaciae,* only one, *Spinacia oleracea* L.,[2] became infected.

The writer did not test *Spinacia tetrandra* for resistance to mildew. This species differs from *S. oleracea* L. in having a varying number of stamens instead of a constant number of four, as in *S. oleracea.*

Until evidence is found to the contrary, suscepts of *Peronospora spinaciae* may be said to be limited to species of Spinacia.

[2]*Spinacia inermis* M. is a smooth-seeded spinach and is listed as a variety of *S. oleracea* by Linnaeus. *S. oleracea* is given as the smooth-seeded form by Vilmorin. The smooth- and prickly-seeded varieties cross readily with each other and are considered by many to be varieties of a single species, *Spinacia oleracea* L.

VARIETAL SUSCEPTIBILITY

There are many varieties of the common garden spinach, *Spinacia oleracea* L., and each year new ones are being developed through breeding and selection. All of the present known commercial varieties may be placed in one of the following four groups: 1, savoy-leaved, round-seeded; 2, smooth-leaved, round-seeded; 3, savoy-leaved, prickly-seeded; or 4, smooth-leaved, prickly-seeded.

At least two workers (Pirone[3], and Guba, 1930) have conducted field tests to determine the susceptibility of several spinach varieties to mildew.

Pirone concluded from his tests that Dark Broad-leaved Prickly (Ferry Morse) and Standwell Prickly (Zwaan and van der Molen) were resistant to mildew, while Bloomsdale Reselected (Zwaan and de Wiljes), and Victoria and Long-standing Gaudry (Zwaan and van der Molen) were the most susceptible.

In the writer's trials, the seven spinach varieties listed by Guba as showing only a trace of mildew, and the two varieties reported by Pirone as resistant, were susceptible to mildew and severely injured by it if they were inoculated under conditions favorable for infection.

Inoculations were made in moist chambers in the greenhouse on thirty-five commercial varieties of spinach representing all the known types; these were equally susceptible to mildew (page 7). As far as the writer has been able to determine, there are at present no commercial varieties of spinach which are genetically resistant to spinach mildew.

THE DISEASE

NAMES APPLIED

Downy mildew of spinach is the name most commonly found in the literature (Clinton, 1916; Hiura, 1929; Guba, 1930; Ramsey, 1935). A few writers call it *spinach blight,* and this term is sometimes used by farmers on Long Island; however, this name more commonly refers to *spinach yellows,* a virus disease of spinach. The name most frequently used by vegetable growers is *blue mold.*

HISTORY AND RANGE

The history and range of spinach mildew often are associated and confused with downy mildews which occur on other members of the Chenopodiaceae. Spinach mildew was first reported from Great Britain by Greville in 1824, where it was abundant around Edinburgh.

According to Eriksson (1918), Magnus found spinach mildew near Berlin in 1887 and apparently it had been there for many years. From 1893 to 1918 it was reported from many sections of Germany. In 1885, W. G. Smith observed it in England. In 1903, N. Ranojevic found it in Serbia, and Noelli found it in Italy in 1906. Halsted reported its presence in the United States in 1890 and later Humphrey and Duggar found and reported it. It is known to have been in Sweden since 1904.

Bisby (1928) wrote that the disease was first found in Canada in 1926. Clinton (1916) reported it from Connecticut. Briton-Jones (1926) reported it from Egypt. Gäumann (1923) reported it on *Spinacia oleracea* in Scot-

[3]Nassau County Farm Bureau Fellowship. Mimeographed repts. 1930 and 1931.

Varieties of spinach tested for susceptibility to spinach mildew

Seed source	*Variety*
Ferry Morse	Prickly-seeded Winter Broad Flanders Long-standing Bloomsdale Juliana Long-standing King of Denmark Virginia Blight-resistant Old Dominion Savoy-leaved, or Bloomsdale Giant Thick-leaved, or Nobel Prickly-seeded Dark Green
Zwaan and van der Molen	Canner King Viroflay Improved Amsterdam Giant Eskimo French Summer Rhineland Giant Standwell Prickly
Sluis and Groots	Long-standing of Enkhuizen (prickly seed) Long-standing of Enkhuizen (smooth seed) Herald Round-leaved Winter Gaudry, or Lettuce-leaved Broad-leaved Ideal Giant Broad-leaved Triumph Long Season Broad-leaved Winter Fillbasket Victoria Eskimo Giant Viking Dark Green Giant Thick-leaved Zenith
F. H. Woodruff	Harlem Market Long-standing Bloomsdale

land, France, Switzerland, Germany (Bavaria, Hessen, Silesia, Thuringia, and Brandenburg), Holland, Austria (Bohemia and Lower Austria), Hungary, Serbia, Northern Italy, Denmark, Sweden, Russia, Japan, China, Argentina, United States, and Canada; and on *S. inermis* in Switzerland.

The range of spinach mildew in the United States is shown on the map below (figure 1). The figures show the number of times spinach mildew has been recorded for each State. The data were taken from *The Plant Disease Reporter* and its supplements, and cover the period from 1918 to 1937. Further search would undoubtedly show that spinach mildew is found wherever spinach is grown.

ECONOMIC IMPORTANCE

Spinach is an important vegetable crop in many countries, and is the most important crop grown for greens in the United States. Data taken from published reports of the United States Bureau of Agricultural Economics

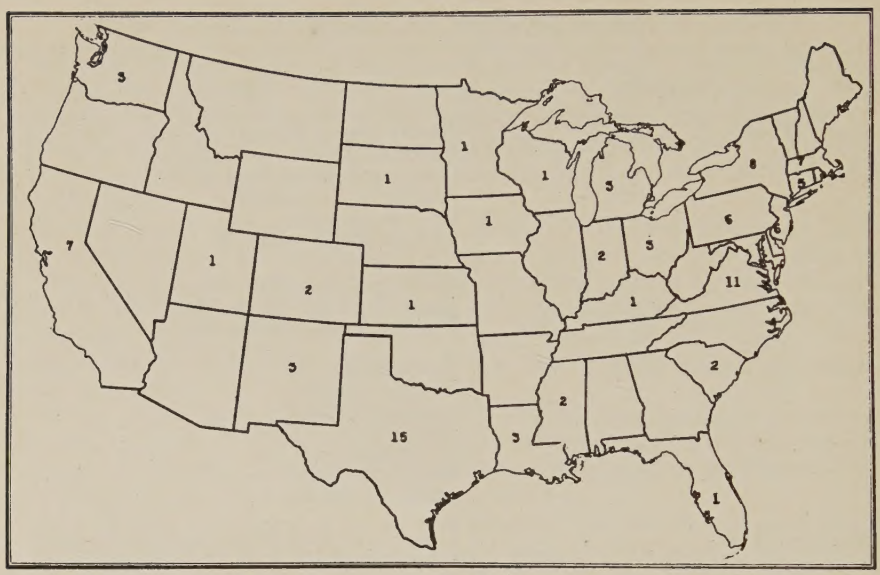

FIGURE 1. RANGE OF SPINACH MILDEW IN THE UNITED STATES AND NUMBER OF TIMES IT HAS BEEN REPORTED FROM THE VARIOUS STATES

show that in 1936 more than 76,000 acres of spinach was grown for marketing fresh, and 27,000 acres for canning. The total value of the crop was approximately $5,953,000. Those States which produce the most spinach for marketing fresh are Texas, Virginia, California, Louisiana, New Jersey, Maryland, and Missouri. Spinach for canning is most largely grown in California.

Spinach mildew is epiphytotic in occurrence. When conditions are favorable for inoculation and infection, the entire crop in the area may be lost in a few days. Losses occur largely in the field, but it may be destructive while the plants are being shipped to market.

No figures are available on mildew losses for the United States as a whole, but losses for the individual States or for important spinach-producing areas within the States are given in *The Plant Disease Reporter* and its supplements. These show that from three to fifteen per cent of the crop planted in the United States each year is not harvested because of this disease.

The spring and fall crops are the most seriously affected by mildew on Long Island. At times the plants become so badly diseased that the farmer must plough under an entire crop. When mildew appears, some growers attempt to harvest the plants even if they are not fully grown. A low yield is thus obtained and the plants may spoil while being shipped to market. Some growers wait, if the weather appears favorable, for the uninfected plants to mature, in the hope of getting a larger yield. But they are likely to suffer further losses or else the spinach harvested is inferior in quality. The losses from mildew in Nassau County are usually from three to eight per cent; but they may go as high as twenty per cent for certain sections, and it is not uncommon for an entire planting to be lost on individual farms.

No data are available on losses from mildew in foreign countries, but workers in Germany, Sweden, and England mention the disease as being important.

MORPHOLOGIC SYMPTOMS

Infected spinach plants are easily identified by the small to large, irregular areas which are differentiated from the healthy leaf tissue by their pale yellow color. The invaded areas do not have sharp margins and they are not bounded by the leaf veins as with the downy mildews of *Chenopodium album* and *C. paganum*. When the plants are old or in a seeding condition the older, lower, leaves become infected.

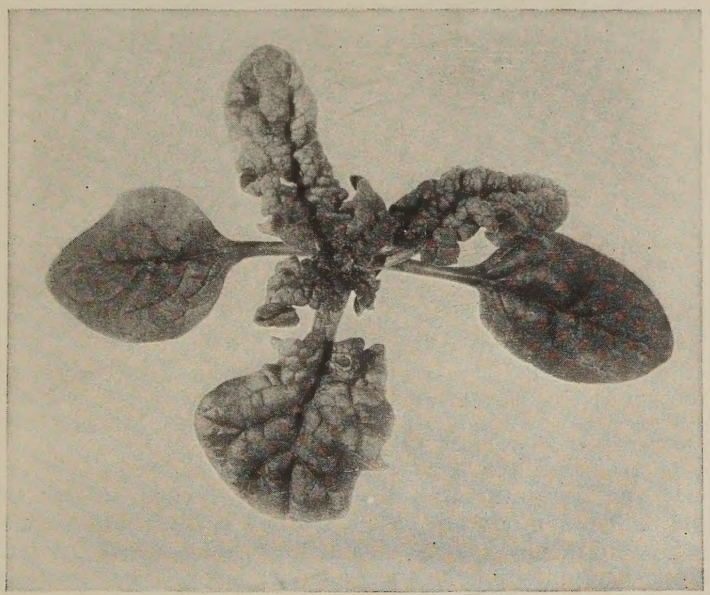

FIGURE 2. A YOUNG SPINACH PLANT SEVERELY INFECTED WITH MILDEW

A distinct yellowing of the diseased areas may occur, during periods of low relative humidity following infection, but fruiting of the fungus may not take place for days or even weeks. Under humid conditions fruiting occurs on the under leaf surface, while the upper surface remains for some time free from any visible symptom of infection. Yellowing of the leaf may follow or precede fruiting of the pathogen. The symptoms are the same on the cotyledons as on the true leaves.

In continued wet weather infected leaves become water-soaked, change rapidly in color to a yellowish brown, and soon rot. Under greenhouse conditions where the plants are succulent and the humidity is high, wilting and death of the leaves take place within four or five days after inoculation. Observations made to determine the tissues involved in infection show that wilting and death of the plant tissues are not always confined to the infected part of the leaf.

Spinach plants weakened by mildew are often attacked in the field by a weak parasite *Heterosporium variable* Cke. (Reed and Cooley, 1911). This fungus produces small, circular, necrotic spots on the mildew-infected areas of the leaves (figure 3).

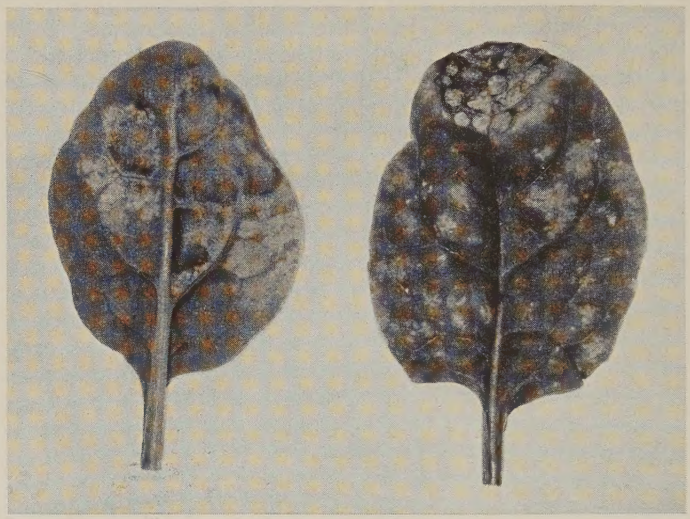

FIGURE 3. SPINACH LEAVES SEVERELY INFECTED WITH MILDEW, VIEWED FROM THE UNDER SURFACE

The tip of the leaf on the right shows the typical necrotic spots caused in mildew-infected leaves by *Heterosporium variable* Cke.

At times, and frequently in the late fall, plants become severely diseased but are not killed by the pathogen. The leaves on such plants are stunted and have a creamy yellow color. Usually they have a savoyed, or puckered, appearance. Those leaves which were mature before they became infected are yellowed but remain normal in shape.

When the fungus fruits, the infected leaf area changes in color from green to a downy white, and later, within a few hours, to a greyish purple. Under very humid conditions it is not uncommon to find the fungus fruiting on both leaf surfaces and the petioles. Yellowing and stunting of the petioles and stems of the plants may also be observed.

Diseased spinach plants which live over winter are readily identified, for they are stunted in growth, their center leaves have a creamy-yellow color, and they are somewhat thicker than normal.

MORPHOLOGY OF THE PATHOGEN

In studying the morphology of the mildew fungus, stained and unstained freehand sections of infected tissues were made, as well as stained microtome sections. Aniline blue (Lepik, 1928) was found to be the best stain for the freehand sections and macerated tissue. Microtome sections from eighteen to twenty microns thick were cut and stained with thionin and orange G or with haemotoxylin and orange G (Rawlins, 1933).

A coenocytic mycelium typical of the Peronosporaceae is formed upon further development of the conidial germ tube. The cylindrical hyphae are large with an average diameter of about 7.03 microns, a single hypha varying in size from 4.8 to 11.1 microns. The hyphal strands are very irregular in shape and have numerous side branches (figure 4, E) which also branch repeatedly in the intercellular spaces of the palisade and mesophyll cells of the leaf and the parenchymatous cells of the petioles and stems. The mycelium of the pathogen has never been observed in the vascular bundles, but it has been found to ramify the intercellular spaces of the parenchymatous tissues of the stem as far as the central pith cavity.

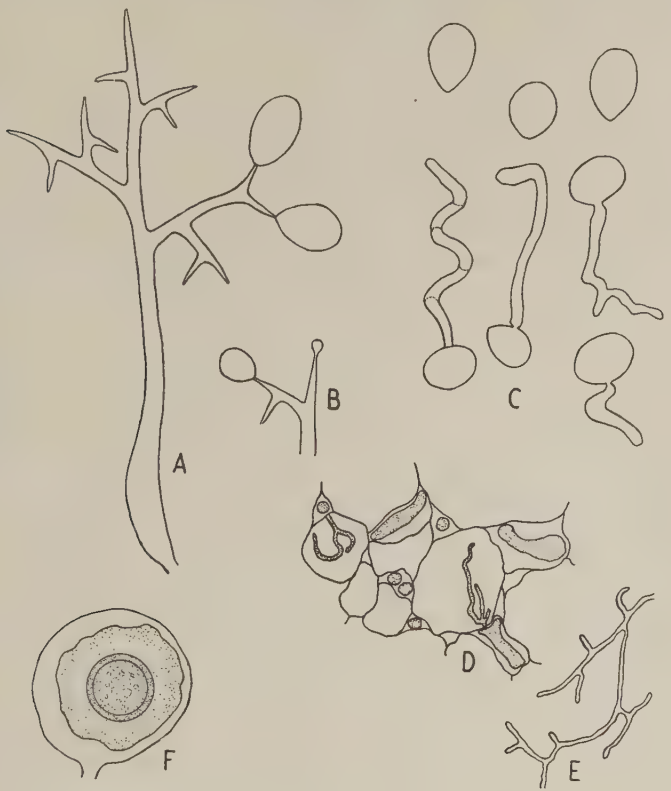

FIGURE 4. MORPHOLOGY OF THE PATHOGEN

A, conidiophore with attached conidia; B, tip of conidiophore with developing conidia; D, infected leaf tissue, showing intercellular mycelium and intracellular haustoria; E, mycelium of the pathogen; F, oospore inclosed in the oogonium

Numerous haustoria arise from the hyphae and develop within the cells to become elongated finger-like organs. The haustorial branches arise at a common junction and may be numerous and long enough to almost fill the cell (figure 4, D).

The conidiophores arise through the stomates on both leaf surfaces, the petioles, stems, and fruits of the plant. They are a greyish purple when viewed macroscopically in mass. The conidiophores are produced either

singly or in fascicles. They vary in length from 200 to 300 microns and are from 9 to 11 microns in width at their base. The main trunk of the conidiophore is straight, seldom undulate as in *Peronospora variabilis* Gäum. From three to five branches arise at acute angles from the main stalk of the conidiophore. Secondary branching is always dichotomous. The tips of the conidiophores are at right angles to the branches, usually straight, but sometimes slightly recurved (figure 4, A).

The conidia vary in size and shape. Those taken from naturally infected plants in the field are ovoid and without a basal papilla. Some conidia are much more granular in appearance than others, but attempts to correlate the appearance of the conidia with their viability were unsuccessful.

The measurements for the conidia of *Peronospora spinaciae* as found in the literature differ greatly from each other and from those obtained by the writer (table 3).

TABLE 3. MEASUREMENTS OF CONIDIA AS GIVEN IN THE LITERATURE FOR THE DOWNY MILDEW PATHOGEN WHERE SPINACH IS MENTIONED AS A SUSCEPT

Author	Date	Range (in microns)	Mean (in microns)
Caspary	(1855)	14–17 × 25–31	15.5 × 28.0
Saccardo	(1888)	16–23 × 25–31	19.5 × 26.0
Schröter	(1889)	16–18 × 20–24	17.0 × 22.0
Fischer	(1892)	17–18 × 22–24	17.5 × 23.0
Schröter	(1897)	20 × 27–36	20.0 × 31.5
Berlese	(1903)	18–21 × 25–34	19.5 × 29.5
Laubert	(1906)	15–21 × 21–29	18.0 × 30.0
Noelli	(1906)	19–20 × 24–31	19.5 × 27.0
Noelli	(1909)	16–20 × 21–24	18.0 × 22.5
Gäumann	(1919)	19.90 × 24–30	19.9 × 27.0
Sorauer	(1928)	19 × 25	19.0 × 25.0
Felix*	(1932)	14–24 × 17–31	20.8 × 26.8
Chu	(1935)	15–22 × 17–27	18.5 × 23.1
†	(1938)	17–26 × 22–38	20.6 × 29.9

*Measurements obtained through correspondence with Mr. Felix.
†Measurements obtained by the writer given for comparison.

To determine if the weather or season had any effect on the size of the conidia, measurements were made during the months of May, June, July, August, and September on conidia taken from naturally infected plants. Measurements also were made on conidia produced in January in the greenhouse. The measurements (table 4) show that the conidia were significantly longer during the months of May and June than during July, August, and September. They were significantly wider during the months of June, July, and August.

The conidia produced in the greenhouse differed only slightly in width from those formed in the field, but they were much shorter, and more nearly globose in shape.

TABLE 4. EFFECT OF SEASON ON THE SIZE OF THE CONIDIA OF *Peronospora spinaciae*

Month	Conidia measured	Range	Mean
May	110	18.0–25.9 × 22.2–34.8	19.98 ± .18 × 30.56 ± .28
June	180	18.1–25.3 × 24.8–36.6	20.20 ± .20 × 30.19 ± .28
July	75	18.9–25.5 × 25.5–35.4	21.46 ± .11 × 29.97 ± .15
August	150	18.5–24.0 × 25.9–37.8	21.94 ± .22 × 29.45 ± .09
September	80	17.0–22.2 × 25.9–33.3	19.54 ± .12 × 29.53 ± .12
January (greenhouse)	102	17.1–24.4 × 22.6–34.0	20.79 ± .11 × 27.82 ± .24

The sexual reproductive organs of *Peronospora spinaciae* are produced in the living infected tissues of the suscept. Just what conditions favor their initiation and development are not known. The oogonium is a spherical almost hyaline organ with a very thin wall. It varies in size from 40.0 to 55.5 microns, and at maturity it forms a permanent layer around the oospore (figure 4, G). The antheridium is a clavate body and according to Hiura (1929) it is usually "Irish potato shaped", 8–14 x 20–30 microns in size.

The oospores are spherical bodies, and at maturity have a thick wrinkled epispore which is a deep yellowish brown in color. Measurements were made on 235 oospores found with the spinach seeds and in infected leaves. They ranged in size from 35.7 to 42.5 microns, with a mean diameter of 36.8 microns. Hiura (1929) found them to have a mean diameter of 30 microns. When treated with sulfuric acid (72 per cent or stronger) the oospore wall gives a cellulose reaction.

Only a few workers have found or described the oospores of the spinach-mildew pathogen. De Bary (1863) described and pictured oospores, and Fischer (1892) described them, but their descriptions were based on material found in species of Chenopodium. Smith (1885) observed the oospores in the decaying tissue of spinach. Duggar, in 1909, and Reed and Cooley (1911) mentioned that they found oospores in abundance in spinach leaves. Eriksson (1918) stated that the fungus did not form oospores, but later described and pictured their germination. Hiura (1929) found and described the oospores of *Peronospora spinaciae*. Ramsey (1935) and Cook (1933, 1935) reported finding the oospores in the leaves of the suscept and with spinach seeds.

Magnus (1887) studied the spinach pathogen in Germany and stated that it did not form oospores. Schröter (1897) was of the same opinion. Laubert (1906), Noelli (1906) and Lanza (1929) did not find the oospores in spinach and believed that they were not formed by the fungus.

It may be concluded from the above reports that the fungus forms oospores only under definite environmental conditions or that it is heterothallic. De Bruyn (1935) showed that heterothallism is a factor in oospore formation by *Peronospora parasitica* (P.) Fr. The writer has never found the oospores of *P. spinaciae* on Long Island but he has found them in leaves obtained from Texas and Virginia.

Isolates of the fungus, which had under natural field conditions formed oospores in infected plants, were obtained from Texas and Virginia. Plants infected with these isolates and with one from plants grown on Long Island were subjected to various conditions of light, temperature, moisture, and nutrition in the greenhouse, but oospores were not obtained. Cook obtained oospores in infected plants in the greenhouse in Virginia.

The writer has found that oospores are commonly produced by the mildew pathogens occurring on *Chenopodium album* and *C. paganum* on Long Island.

ETIOLOGY

Classification, name, and history of the pathogen

The spinach-mildew fungus is a member of the genus Peronospora. The disease and its causal organism were first described by Greville (1824) in Great Britain. He named the fungus *Botrytis effusa*. This name has no

standing, except in synonomy, because it appeared before 1832, the year in which volume III of Fries' *Systema mycologicum*, the starting point for the nomenclature of this group, was published. Fries does not list the spinach pathogen. He records *Botrytis farinosa*, found on one or more species of Atriplex. This fungus is a species of Peronospora, and the only one recorded by Fries that is closely related to the spinach pathogen.

Desmazieres (1837) applied the name *Botrytis effusa* Grev. to a fungus on Chenopodium and redescribed the species from material on this suscept. He also included as suscepts species of Atriplex, Urtica, and Rhynanthus, and suggested that Fries' *Botrytis farinosa* on Atriplex and Greville's *B. effusa* on spinach were the same fungus.

Rabenhorst (1854) lists number 1880 in *Klotzchii Herbarium vivum mycologicum* under the name *Peronospora (Botrytis) effusa* Cesati. On the label of the specimen the following information is given:

Nr. 1880
a). on *Chenopodium* sp., Vercelles, 1852, Cesati
b). on *Chenopodium album*, Frankfurt a. M. 1853
A. de Bary.

Although Rabenhorst uses Greville's specific name, in transferring the fungus from Botrytis to Peronospora, he designates a Chenopodium and not spinach as the host. The fungi occurring on spinach and *Chenopodium album* are distinct species. Therefore, Rabenhorst should not have used the name *effusa*, for it was used first by Greville as the specific name for the spinach pathogen. The name *Peronospora effusa* (Grev.) Rabh. most commonly found in the literature is incorrectly applied to the spinach pathogen.

Caspary (1855) was the first mycologist to call attention to the fact that morphological differences exist among the various downy-mildew pathogens on species of the Chenopodiaceae. He established "major" and "minor" varieties for *Peronospora effusa* Rabh. According to Gäumann, Caspary did not study the spinach fungus, although he included it in his "major" variety.

De Bary (1863) used Rabenhorst's binomial *Peronospora effusa* (Grev.) Rabh. He recognized Caspary's work, and listed a variety "major" with *Chenopodium album, C. hybridium,* and *Spinacia oleracea* as suscepts; and a variety "minor" with *Atriplex patula, C. polyspermum,* and *Spinacia oleracea* as suscepts. For many years mycologists followed de Bary in using the binomial *Peronspora effusa* (Grev.) Rabh. with the "major" and "minor" forms.

Laubert (1906) studied the mildew pathogen occurring on *Spinacia oleracea* and *Chenopodium album* and found them to be morphologically different; therefore, distinct species. He described the spinach pathogen and named it *Peronospora spinaciae*. He did not find the perfect stage of the fungus, but since this was the first time that the spinach fungus had been named and described since the time of Fries, Laubert's binomial should be used.

Noelli (1909) studied the conidia of the downy mildews found on spinach and *Chenopodium album* and decided that they were the same species. He found basal papillae on the conidia taken from spinach. They have not been found by the writer or reported by others, so it is possible that Noelli's material may have become contaminated in some way.

Wilson (1914) believed that the "major" and "minor" varieties established by Caspary for *Peronospora effusa* should be raised to species rank. Variety "major" became *P. effusa* (Grev.) Cesati, with Chenopodium as the suscept. Variety "minor" became *P. farinosa* (Fries) Keissler, with Atriplex as the host. Wilson listed spinach as a suscept for both species.

Eriksson (1918) used the binomial *Peronospora spinaciae* (Grev.) Laubert. Greville's name should not be given as authority for the species name.

Gäumann (1919) found that the mildews occurring on the Chenopodiaceae could not be separated into two varieties or species on the basis of the branching of the conidiophores and the shape of the conidia. Some of the fungi would fall into one or the other of the varieties quite readily; others were intermediate in type and could not be placed with certainty. For example, the spinach pathogen was placed in variety "major" by Caspary, Fuckel, and Saccardo; Fischer, Berlese, and Magnus listed it in the variety "minor". Wilson and de Bary placed it in both varieties.

Gäumann (1919) studied the conidia taken from twenty species of the Chenopodiaceae. He determined the widths and lengths of five hundred conidia, and plotted distribution curves for each set of measurements. From these curves he established fourteen species. It is doubtful that other workers could use Gäumann's method for species determination and obtain the same results that he did. Evidence has been given (page 12) to show that environmental conditions may affect the size of the conidia. From figures 5 and 6 it is apparent that the curves obtained by Gäumann are distinctly different from those obtained by the writer.

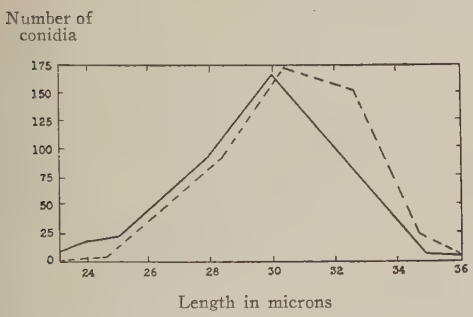

FIGURE 5. DISTRIBUTION CURVES FOR THE LENGTHS OF 500 CONIDIA OF PERONOSPORA SPINACIAE

—— curves from Gäumann
- - - - curves obtained by the writer

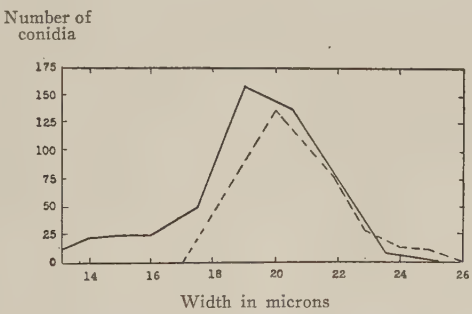

FIGURE 6. DISTRIBUTION CURVES FOR THE WIDTHS OF 500 CONIDIA OF PERONOSPORA SPINACIAE

—— curves from Gäumann
- - - - curves obtained by the writer

Studies were made by the writer on mildew pathogens taken from six species of Chenopodium, two species of Atriplex, and from spinach. It was found that the conidiophores varied in size, shape, and branching; and that the conidia were decidedly different. Some of them were papillate and others were not. Fresh material and herbarium specimens were examined, and a provisional key based on morphologic differences of the pathogen was made which would enable one to separate the nine fungi studied into eight species.

Pathogenicity

Hiura (1929), Schaffnit and Volk (1927), Cook (1935), and others have demonstrated the pathogenicity of the spinach-mildew fungus. The writer made numerous successful inoculations with the conidia, but was never able to obtain infection of healthy spinach plants when he inoculated their leaves with oospores obtained from infested spinach seeds.

Life history

Peronospora spinaciae is an obligate parasite; its entire life cycle of growth and reproduction is spent in association with a living spinach plant. Saprogenesis does not occur unless the short period of growth during germination of the oospores is considered to be saprophytic. This has been suggested for the oospore germination of *Peronospora Schleideniana* Smith by McKay (1937).

After the completion of the primary cycle, an indefinite number of secondary cycles occur during the growing season for spinach. The number of cycles and the duration of each are determined by the weather and the availability of the suscept.

Sources of the primary inoculum

The conidia are the most important inoculum for both the primary and secondary cycles of the pathogen on Long Island. Tests made to obtain information on the rôle of the oospores as inoculum were unsuccessful.

There are five possible sources of the primary inoculum: 1, weed suscepts; 2, infected seeds; 3, infested seeds; 4, infested soil; and 5, infected spinach plants which overwinter.

1. *Weed suscepts.* A list of the plants, most of which are common weeds, that have been reported by various writers as suscepts of the spinach pathogen has been given (table 1). Inoculation tests made by Schaffnit and Volk (1927), Hiura (1929), Leach (1931), Cook (1936), and the writer, on the plants listed in table 2 showed that none of them except plants in the genus Spinacia were susceptible to *Peronospora spinaciae.*

Magnus (1887) believed that *Peronospora spinaciae* overwintered on spinach and spread from it in the spring of the year to Atriplex and Chenopodium. Evidence has been presented by the writer (table 2) to show that this phenomenon does not occur, and no positive evidence has yet been found to show that the mildew pathogens occurring on species of the Chenopodiaceae will infect spinach. The possibility that weeds act as a source of the primary inoculum may be eliminated.

2. *Infected seed.* Seed transmission of downy-mildew pathogens has been demonstrated in only a few cases. The hyphae of the fungi have been found in the seeds of their suscepts, but it has been difficult to demonstrate that the mycelium present really functioned as inoculum. Wolf and Lehman (1924) found circumstantial evidence that *Peronospora manschurica* was transmitted in soybean seeds. Angell demonstrated transmission of *P. tabacina* in seeds of tobacco, but Leach (1931) working with *P. spinaciae,* did not obtain positive results on transmission. Circumstantial evidence for seed transmission of *P. destructor* was reported by Newhall (1938).

Cook (1933) and Leach and Borthwick (1934) found the mycelium of the spinach-mildew pathogen in spinach seeds. Cook observed it in the pericarp, funiculus, and integuments of the ovule, and Leach and Borthwick found the hyphae in the calyx tube, funiculus, integument, and nucellus.

Leach planted ten lots of infected spinach seed in steam-sterilized soil and obtained 1260 seedlings. Seventy days later no mildew was found on the plants. In another test made by Leach, eight lots of infected seed from commercial sources produced 1230 plants but none of them developed mildew.

Positive evidence has not been produced to show that infected seeds are a source of the inoculum, but since the mycelium of the pathogen has been found frequently in the seeds, seed transmission under field conditions may be important.

3. *Infested seeds.* Cook (1936) pointed out that the oospores of *Peronospora spinaciae* are present in commercial samples of spinach seed. The writer also found this to be so. Eighty samples of seed were obtained from fourteen seed dealers. The samples varied in weight from one-half to ten pounds. Each sample was shaken over a fine mesh screen, and the screenings were collected and weighed. About one milligram of the screenings from each sample was then placed in water on a slide and observed with the aid of a microscope. The number of oospores per pound of seed was determined. Oospores were found in seventeen of the eighty samples, and the conidiophores of the pathogen were in two more (table 5).

TABLE 5. SPINACH VARIETIES WHOSE SEEDS WERE INFESTED WITH THE OOSPORES OF *Peronospora spinaciae*

Variety	Seed sample (pounds)	Estimated oospores per pound of seed
Long-standing Enkhuizen	½	600
Gaudry	½	180
Ideal, Giant Broad-leaved	½	2320
Long Season	½	1440
Giant Thick-leaved	½	10
Zenith	½	420
Canner King	1	Conidiophores
Rhineland Giant	1	720
Viroflay Improved	1	400
Eskimo	1	250
Hollandia	1	10
Harlem Market	5	41
Darkgreen Bloomsdale	10	20
Princess Juliana (1935)	1	1320
Princess Juliana (1936)	1	260
Princess Juliana (1937)*	5	750
Princess Juliana (1937)*	1	200
Special Thick-leaved	5	Conidiophores
Long Season	5	10
King of Denmark	1	1500

*From two different sources.

Seeds from fourteen of the varieties containing oospores were planted in four-inch pots in the greenhouse under conditions favorable for the development of mildew. They were kept in a greenhouse maintained at a temperature of 60–70° F. in a crowded condition with plenty of moisture. Screenings containing oospores were added to the soil. At the end of sixty days none of the plants had developed mildew.

4. *Infested soil.* The writer has never found oospores in the leaves of infected spinach plants on Long Island. They may be produced, but a systematic search has failed to reveal them. In 1937, 440 leaves obtained from various parts of Nassau County were examined for oospores. Similar investigations were made in 1935 and 1936, but oospores were not found. Attempts have been made to produce oospores in infected leaves by leaving them in moist chambers at various temperatures. Severely infected plants were left in the ground in a container to overwinter in 1935–36, but no oospores developed.

On May 18, 1937, 117 sections made from fifty leaves received from Norfolk, Virginia, were examined and four were found which contained numerous oospores. No oospores were found in twelve leaves received from Virginia on December 15, 1937. On January 7, 1938, fifty leaves were received from Winter Haven, Texas, and in ten of these numerous oospores were found.

Ramsey (1935) reported finding oospores in wind-whipped Texas spinach. He did not report finding them in plants shipped in from other sections of the United States. The writer is of the opinion that when the oospores of *Peronospora spinaciae* are produced they are formed in infected living host tissue and not in dead tissues as reported by Wolf (1934) for *Peronospora tabacina.*

Under conditions where numerous oospores are formed it is readily seen that the soil may become infested with them, but until more is known regarding the germination and longevity of the oospores their importance as inoculum when in the soil has yet to be determined.

5. *Infected overwintered plants as a source of the inoculum.* It is a common practice for farmers on Long Island to plant spinach seed in the late summer. The plants which develop winter over and are ready for harvest in April and May. If these plants become infected in the fall the pathogen lives through the winter in the plant tissues. In the spring when conditions of moisture and temperature are favorable, the fungus produces conidia and these initiate the primary cycle. The importance of these infected overwintering plants as a source of inoculum is shown by the fact that on 24 farms (15 in 1936 and 9 in 1937) where such plants overwintered, mildew developed in the winter-sown and spring-sown crops. On the other hand no mildew was found on 9 farms (6 in 1936 and 3 in 1937) where spinach was not overwintered.

Diseased spinach plants are the most important source of the primary inoculum on Long Island. Infected seed, infested seed, and infested soil may be sources of the primary inoculum, but their importance has not yet been determined.

Sources of the inoculum for later cycles of the pathogen

Severely infected spinach plants may be found during the entire spinach season. The presence of mildew during the summer indicates that there are many cycles in the life history of the pathogen. The conidia produced during each cycle act as inoculum to initiate later cycles of the fungus.

Agents of inoculation

The conidia of the pathogen are disseminated by the wind and rain. Spore traps were placed in a field where many of the plants were infected

with mildew. They were placed one foot, two feet, and three feet above the ground. After forty-eight hours the traps were washed with water and the washings examined for conidia. Three trials were made and each time numerous conidia were found in the washings. The studies show that the conidia are carried by the wind and they may at times be found in the air in great numbers.

Rain is an important agent of inoculation since it splashes the conidia from leaf to leaf and onto the under surfaces of the leaves where they cannot be reached by a fungicide. The oospores in the ground may also be splashed or washed onto the leaves by the rain.

Factors which influence conidial germination

The conidia of *Peronospora spinaciae* always germinate by the production of a single germ tube which seldom branches (figure 4, C). It arises from the side of the spore, and as it elongates the protoplasm flows out into the germ tube so that eventually the conidium and the lower part of the tube contain no protoplasm. In water on glass slides the germ tube may reach a length of almost a thousand microns before growth stops.

1. *Water.* Free water is necessary for spore germination. Attempts to germinate viable conidia of the fungus in high relative humidities at 60° F. were unsuccessful. Care was taken to avoid condensation of moisture on the spores during the trials. The conidia did not germinate when removed and placed on glass slides or when left on the leaf of the suscept under conditions of high relative humidity.

2. *Age of the conidia.* Cook (1936) found that the conidia of *Peronospora spinaciae* did not germinate as well immediately after they were formed as they did a day later. Tests were made by the writer to determine the effect of age of the conidia on germination. The results are given in table 6.

TABLE 6. RELATIONSHIP BETWEEN THE AGE OF THE CONIDIA AND THEIR GERMINATION

	Age of the conidia in days			
	0	1	2	3
	Per cent of germination			
Plant 1	58.9	68.2	43.9	0.1
Plant 2	42.5	53.2	1.8	0.3
Plant 3	44.6	52.2	9.9	0.0
Plant 4	67.6	71.1	9.5	0.0
Average	53.4	61.1	16.0	0.1

In another test the conidia remained viable for nine days. The conidia produced during the night of January 10–11, 1938, were left undisturbed on infected leaves in the greenhouse. The temperature for the period ranged between 60° and 70° F., and the relative humidity between 50 and 85 per cent. The results are recorded in table 7.

3. *Temperature.* Studies were made to determine the optimum temperature for conidial germination. The conidia were washed from infected spinach leaves with distilled water, and drops of this suspension were placed

TABLE 7. EFFECT OF AGE OF THE CONIDIA ON THEIR GERMINATION

Age of the conidia in days	Per cent of germination
0	82.0
1	51.0
2	48.0
7	7.4
9	4.6

on clean glass slides in moist chambers. The moist chambers and slides were pre-cooled and held at temperatures of 3, 6, 9, 12, 15, 18, 21, 24, and 27° C. Eighteen hours later germination counts and measurements on the length of the germ tubes were made (figures 7 and 8). The optimum temperature for germination was about 9° C. (48.2° F.); germ-tube elongation was greatest at 12° C. (53.6° F.). The minimum temperature at which germination took place was about 2° C. (35.6° F.), and the maximum at 27° C. (80.6° F.); Hiura (1929) gave the minimum as 3° C., the optimum at 8° to 10° C., and the maximum at 30° C.

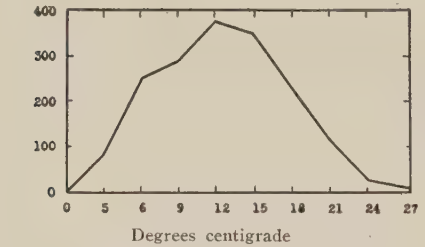

FIGURE 7. EFFECT OF TEMPERATURE ON THE ELONGATION OF THE GERM TUBE

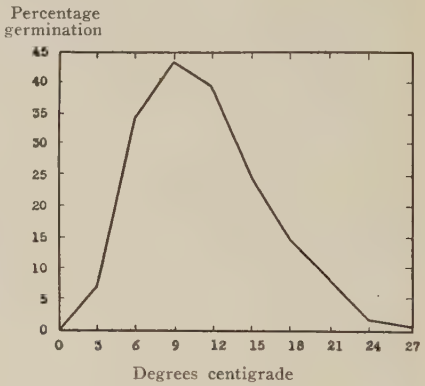

FIGURE 8. EFFECT OF TEMPERATURE ON GERMINATION OF THE CONIDIA

When placed in water at their optimum temperature for germination, 9° C. (48.2° F.), the conidia will start germinating within one to one and one-half hours, and all of the viable conidia will have germinated within five hours. Hiura found one to one and one-half hours necessary for germination at 10° C.

4. *Effect of desiccation on conidial germination.* To obtain information on the effect of desiccation on the conidia, six tests were made in which a water suspension of the conidia was placed on clean glass slides, the water was permitted to evaporate, and the spores were left to desiccate at a temperature of 75° F. After given periods of time, distilled water was added to the spores to permit germination. The spores collapsed when desiccated, but regained their turgor when replaced in water. Short periods of desiccation greatly decreased the viability of the conidia (table 8).

Conidia removed from infected leaves and placed on glass slides were exposed to the sun for periods of time up to 60 minutes. Water suspensions

TABLE 8. EFFECT OF DESICCATION ON GERMINATION OF THE CONIDIA

Minutes desiccated	Number of tests					
	1	2	3	4	5	6
	Per cent of germination					
Check	62.8	77.3	65.0	45.7	36.0	70.0
5	18.2	27.5	5.4	12.4	...	...
15	11.2	17.3	4.7	...	8.8	22.0
25	...	8.7	1.6	14.7	11.8	...
45	8.5	6.0	0.3	...	...	4.0
60	6.7	...	0.0	...	...	2.1
90	...	...	...	...	...	1.5

of the conidia on glass slides were exposed to the sun for as long as 90 minutes. The germination was greatly decreased after short periods of exposure to sunlight, as shown in table 9.

TABLE 9. EFFECT OF SUNLIGHT ON GERMINATION OF THE CONIDIA

Minutes exposed	Conidia dry during exposure		Conidia wet during exposure			
	1	2	1	2	3	4
	Per cent of germination					
Check	66.1	70.3	66.5	66.2	84.0	71.2
5	13.3	...	35.4	61.0	...	...
15	...	8.0	15.0	21.0	84.0	...
30	11.2	5.0	...	...	80.0	21.0
60	5.1	...	...	...	...	...
90	...	...	...	...	...	8.4

Ingress of the germ tube, and the infection courts

Studies were made to determine whether the germ tube entered the suscept through the stomates or by penetration of the cuticle and epidermis. Stomates are located on both surfaces of the leaves and on the fruits of the plant.

Leaves of the suscept were placed in petri dishes and inoculated with a suspension of the conidia. The leaves were held at 12° C. (53.6° F.) for four days and then removed and cut into sections. The sections were placed in formalin-acetic-alcohol for twenty-four hours or longer. They were then stained in anilin blue and studied under a binocular microscope. It was found that penetration takes place through the cuticle at a junction of the epidermal cells. Entrance of the germ tube by way of the stomates as reported by Halsted (1890) was never found.

Both the upper and lower surfaces of the leaves, the petioles, and the stem of the plant may serve as infection courts (table 10). For some reason not determined by the writer, the older lower leaves are much more susceptible to infection than are the younger ones near the top of the plant.

From a single point of ingress the fungus may ramify the intercellular spaces of an entire leaf. Leaves were inoculated with a single drop of water containing conidia. Later, when the fungus fruited, the under surface of the leaf was almost entirely covered with the fruiting structures.

TABLE 10. UPPER AND LOWER LEAF SURFACES AS INFECTION COURTS

Trials	Upper surface			Lower surface		
	Inoculated–		Infected leaves	Inoculated–		Infected leaves
	Plants	Leaves		Plants	Leaves	
1*	2	9	3	2	4	4
2*	2	8	8	2	10	8
3†	2	9	9	1	4	4

*Conidia were atomized onto the leaves.
†Inoculum was placed on the leaves with a dropper.

Two tests were made to determine how long it takes after the plants are inoculated for the conidia to germinate and the germ tube to enter the leaf. Under the temperature conditions used (60°–65° F.) it was found that penetration takes place in less than three hours after the plants are inoculated. This indicates that infection may readily take place in the field, for many times during the spinach season favorable temperatures for infection exist, and the plants are wet with rain or dew for longer than three hours.

TABLE 11. STUDIES ON INFECTION*

Hours that the plants were wet	Plants inoculated	Leaves inoculated	Leaves infected
1–2	2	13	11
2–3	2	15	15
3–4	2	14	10
4–5	2	23	21
5–6	2	13	10

*Plants inoculated March 14, 1938; data taken March 23, 1938. Temperatures, 60° to 95° F. Relative humidity 40 to 95 per cent.

Period between inoculation and fruiting of the fungus

The fungus may produce conidia on the under surface of the leaves before symptoms of the disease can be observed, but for a given set of environmental conditions the length of time which elapses between inoculation of the plant and fruiting of the fungus can be accurately determined. The duration of this period is controlled by at least three factors: temperature, relative humidity, and the general vigor of the plant. In the greenhouse, with relative humidities of 70 to 90 per cent and with temperatures of 60° to 75° F., the shortest period was six days. During the tests, the inoculated plants were placed in the moist chamber each day, beginning with the third day after inoculation, but in no case did fruiting occur in less than six days, and in most cases the period was longer. Schaffnit and Volk (1927) found the period to be between six and seven days.

Free water on the leaf is not necessary for the production of the conidiophores. The fungus will fruit over a wide range of temperatures if the relative humidity surrounding the leaf is 85 per cent or above. Infected plants have been kept in the greenhouse for as long as twenty-one days in relative humidities below 80 per cent without the fungus fruiting, but when the plants were placed in chambers where the humidity was near

saturation, conidia were formed on the plants within twelve hours. The period between inoculation and fruiting may be weeks or even months in duration, for plants infected in the fall may not show fruiting of the fungus until spring of the following year. The relative humidity is usually higher on the under surface of the leaf. This is probably the reason why fruiting of the fungus most commonly occurs on the lower surface of the leaf under field conditions.

EPIPHYTOTICS OF THE DISEASE

Studies and observations made during the past four years show that the following conditions exist when epiphytotics of spinach mildew occur on Long Island.

1. At the time of inoculation the plants are in a vigorous growing condition.
2. Numerous conidia are produced so that many plants are inoculated simultaneously.
3. Mean temperatures of 40° to 50° F. are maintained for a week or more.
4. Water is present on the leaves of the plants from rain, dew, or irrigation for periods of three hours or longer.
5. Periods of high relative humidity exist during inoculation and fruiting of the pathogen.

Spinach, like other plants, has certain optimum conditions for growth. Spinach plants remain in a vegetative condition longer when the days are short and the weather is cool. Spinach reacts quickly to changes in soil fertility or soil acidity. Observations made in June 1937 on soil-acidity plots showed that where the soil acidity was favorable for the growth of the plants, mildew was present in abundance. On the other hand, the incidence of mildew was less on those plots where the plants were adversely affected by the soil acidity.

Under the conditions of the test it was found that at pH 6.2 to about 6.8 the spinach plants attained their maximum growth and best color. With an increase in pH above 6.8, the growth of the plants was not greatly retarded, but they were more upright, slightly etiolated, and less savoyed and yellowed. The highest percentage of mildew was found on those plots where the plants were growing at their optimum soil acidity. It is not a change in the pH of the plant sap which prevents infection, for the acidity of the soil does not affect the acidity of the spinach sap.[4]

Plants which have been injured by rain or wind are less susceptible to attack. In September 1936 and in August 1938 heavy rains and severe wind storms caused considerable damage to spinach in Nassau County. Although favorable conditions of temperature and moisture existed, very little mildew could be found in the county after the storms. As new plants developed and abundant inoculum was produced, epiphytotics of the disease occurred. Attempts to inoculate plants that were not in a vigorous growing condition always resulted in failure.

Mildew is most abundant on Long Island during the months of April, May, June, September, and October, because the mean temperatures during these months are not only favorable for the growth of the suscept,

[4][Anonymous]. Univ. Idaho Agr. Exp. Sta. Bul. 179:12. 1931.

but for the pathogen as well. The optimum temperature for germination of the conidia is about 48.2° F., but infection may take place at temperatures between 40° and 75° F. It will be noted in figure 9 that the mean temperatures for July and part of August are too high for growth of the pathogen, and as a result mildew is seldom severe during these months.

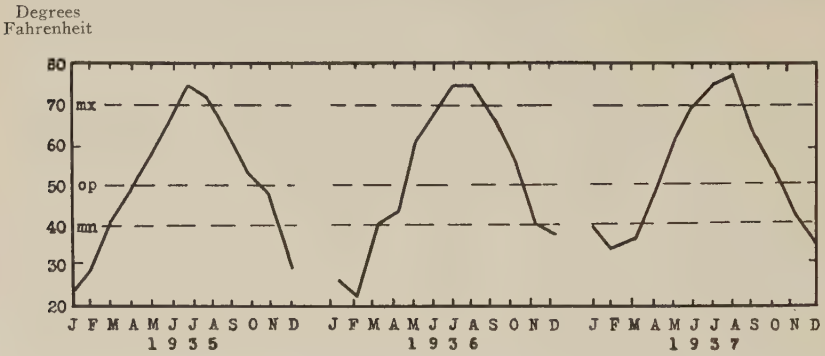

FIGURE 9. MONTHLY MEAN TEMPERATURES TAKEN AT HICKSVILLE, NEW YORK, SHOWING THE RELATIONSHIP BETWEEN THEM AND THE OPTIMUM, MAXIMUM, AND MINIMUM TEMPERATURES FOR THE GERMINATION OF THE CONIDIA OF PERONOSPORA SPINACIAE

The normal rainfall for the months in which mildew is most abundant is above 3.2 inches (figure 10). The plants are not only wet by rain, but also by irrigation water, and this, coupled with the generally high relative humidities which occur on Long Island, furnish ideal conditions for mildew infection.

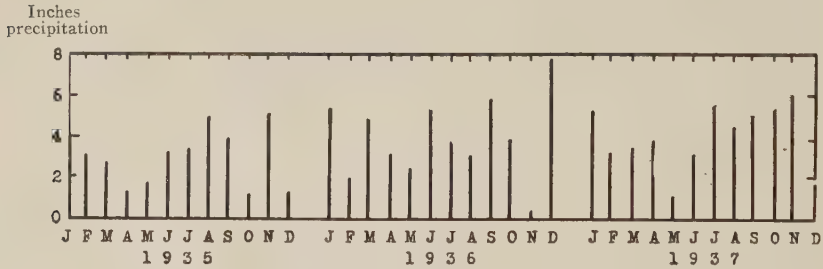

FIGURE 10. MONTHLY PRECIPITATION FOR NASSAU COUNTY, NEW YORK; DATA TAKEN AT HICKSVILLE

CONTROL

The role of infected or infested spinach seed as a source of inoculum has not been determined, for in all of the tests that have been made no positive evidence of seed transmission has been obtained. Circumstantial evidence gathered from field studies indicates that infested seeds may be important sources of the primary inoculum.

Downy-mildew pathogens found on chenopodiaceous weeds will not infect spinach; thus the eradication of these weeds would be of no value as

a control measure. Crop rotation should prove worth while although the length of time that the oospores will remain viable in the soil is not known. The separation of overwintered spinach from winter and spring plantings will greatly help the Long Island farmer to prevent losses from mildew.

The protection of the plants with fungicides has been tried by several workers including the writer. Smith (1921) applied a copper-sulfate fish-oil soap with a power sprayer and reduced the number of infected plants by 28 per cent. Pirone[5] used bordeaux mixtures 2–2–50 and 4–4–50, a copper soap spray, and two sulfur dusts on separate plots, but was able to reduce the incidence of mildew by only 10 per cent. The writer used copper oxide (cuprocide 54, 1.75 pounds in 50 gallons of water) on replicated plots and reduced the number of infected plants from 13.4 to 3.9 per cent. The plants were injured slightly by the copper. To protect spinach from mildew by spraying or dusting with a fungicide, both leaf surfaces must be covered.

The use of resistant varieties as a control measure. To find whether there were any mildew-resistant varieties or resistant individuals within the susceptible varieties, a number of plants from each of thirty-five commercial selections were grown in the greenhouse and inoculated with conidia from the pathogen (page 7). Plants in each of the four spinach types described on page 6 were tested and all were found to be very susceptible to mildew. No genetic resistance to the pathogen was found in any of the commercial varieties used in the tests. As a result, the selection of resistant plants for the development of resistant lines was not possible.

SUMMARY

Because of the importance of spinach mildew to vegetable growers in Nassau County, New York, studies on the control of the disease and the life history of the causal organism were made during the years 1934 to 1938.

More than twenty-six species of plants distributed in five families have been reported to be suscepts of the pathogen. Fifteen species from eight genera of the Chenopodiaceae and three species of Amaranthus were used in inoculation tests, but none of them became infected.

Thirty-five commercial spinach varieties were tested and found to be equally susceptible to spinach mildew. As a result of the studies it is believed that the host range of the spinach pathogen is limited to members of the genus Spinacia.

Spinach mildew has been reported from nearly every country where spinach is grown. It has been found in twenty-four States in the United States, where it causes losses of from three to fifteen per cent of the crop each year. Losses of from three to eight per cent occur yearly on Long Island.

Symptoms of the disease are yellowing, stunting, and necrosis of the infected areas.

The morphology of the pathogen was studied in detail. It was found to differ from the downy-mildew fungi occurring on other chenopodiaceous

[5]Nassau County Farm Bureau Fellowship. Mimeographed rept. 1930.

plants. Evidence is given to show that *Peronospora spinaciae* Laubert is the valid name for the pathogen.

Of the four possible sources of the primary inoculum (infected seeds, infested seeds, infested soil, and infected plants which overwinter), the last-named source only was found to be important on Long Island. Wind and rain are the important inoculating agents.

The effect of water, age of the conidia, temperature, and desiccation were studied in relation to the germination of the conidia.

With favorable temperatures, infection may take place in less than three hours after the plants are inoculated. Fruiting of the fungus will not occur in less than six days after inoculation at temperatures of 60° to 70° F. High relative humidities (85 per cent or above) are necessary for fruiting of the fungus.

Studies showed that a combination of the following conditions resulted in epiphytotics of the disease: when inoculated the plants were in a vigorous growing condition; abundant conidia were produced so that many plants were inoculated simultaneously; mean temperatures of 45° to 65° F. were maintained for a week or more; water was present on the leaves for periods of three hours or longer; and high relative humidities existed during infection and fruiting of the fungus.

Control of the disease by isolation of the overwintered spinach plants from the winter- and spring-sown crops is suggested for Long Island farmers. The use of copper fungicides as protectants and the selection of spinach varieties for resistance to mildew proved unsuccessful.

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